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Research Article

Craspedostauros nazmii sp. nov., a new diatom species (Bacillariophyta) from the Turkish Coast of the Black Sea

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Abstract

Craspedostauros E.J. Cox is a diatom genus comprising 17 taxa reported from various regions of the world. While many species of *Craspedostauros* are epibiontic, the taxa have variable ecological preferences. In this study we formally describe *Craspedostauros nazmii* **sp. nov.**, an epilithic species discovered along the Turkish Black Sea Coast, based on light and scanning electron microscopy. *Craspedostauros nazmii* **sp. nov.** is characterized by valves that are lanceolate to narrowly lanceolate, slightly constricted near the apices with uniseriate, parallel throughout the whole valve, transapical striae and and the presence of an apical silica flap. The areolae are distributed over the valve face and the mantle. The differences and similarities between *C. nazmii* **sp. nov.** and established species of *Craspedostauros* are discussed. Based on shape and morphometrics, the most similar species is *Craspedostauros capensis*, but it is easily distinguished from *C. nazmii* **sp. nov.** by its lack of an apical silica flap.

Key words: Apical silica flap, Black Sea, *Craspedostauros*, epilithic marine diatom

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Introduction

The genus *Craspedostauros* E.J.Cox, 1999 was established to accommodate several marine species previously included in *Stauroneis* Ehrenberg (Lange-Bertalot and Genkal 1999; Cox 1999). As the latter genus comprised mostly freshwater species, a separation was proposed by different authors to accomodate the marine species with regards to their autecology and morphological differences. Species strictly conforming with *Stauroneis* Ehrenberg are characterized by naviculoid valves with two girdle appressed chloroplasts and possess a distinct and large central area called stauros (Round et al. 1990). The valves in *Stauroneis* are flat and the girdle is composed of a few plain copulae that is always rather narrow (Krammer and Lange-Bertalot 1986; Round et al. 1990; Cox 1999).

When establishing the genus *Craspedostauros*, Cox (1999) referred to cytological (shape and number of chloroplasts) and ultrastrutural characteristics (cribrate occlusions of areolae), also leading her to point out an affinity with *Mastogloia* Thwaites ex W. Smith (1856). With regards to these affinities,

Craspedostauros has been included in Mastogloiaceae with a recommendation to also move *Achnanthes* Bory *sensu stricto* (Cox 1999; Cox and Williams 2006) there. The molecular phylogeny published by Ashworth et al. (2017) and inferred from a 3 genes dataset (*18S*, *rbcL* and *psbC* genes) tends to associate *Craspedostauros* to *Achnanthes* and *Staurotropis*, but clearly distinguishes them from *Mastogloia* spp., strongly questionning the monophyly of the Mastogloiales. This group of genera was later referred to as CAS genera, for *Craspedostauros-Achnanthes-Staurotropis* by Mann et al. (2021), whose phylogenetic works surprisingly tended to associate the CAS genera with Bacillariaceae. However, the lack of support at the nodes or strong morphological evidences led the authors to consider this result unlikely, probably resulting from an artefact of genes/species sampling and they emphasized the need for deeper phylogenomic investigations in order to elucidate the position of the CAS genera.

As a genus, *Craspedostauros* is relatively small, with 15 taxonomically accepted species listed on AlgaeBase, to which could be added two recently described taxa from Antarctica (Trentin et al. 2022). Thus, there remains a potential for the description of new species in unexplored habitats such as tropical coasts and biofilms on seaweeds in particular (Risjani et al. 2021; Witkowski unpublished observations).

The Turkish Republic is surrounded by four different seas, namely the Eastern Mediterranean Sea, the Aegean Sea, the Marmara Sea and the Black Sea. *Craspedostauros decipiens* was found in the Sea of Marmara (Witkowski et al. 2000; Akçaalan and Kaleli 2021) but this is so far the only species of *Craspedostauros* discovered in Turkish Black Sea waters. The Black Sea is a semi-closed sea located in southeastern Europe. It is considered an isolated sea since the Dardanelles and Bosphorus straits limit water exchange with the Mediterranean Sea. This semi-closure influences both sea water characteristics (typically salinity) as well as the dispersal potential of aquatic species inhabiting both sides of the straits (Nevrova et al. 2013). Studying the diatoms of the Black Sea may be of additional interest for science in that they may represent flora of an ancient marine basin isolated due to limited water exchange over a fairly long geological time period (Witkowski et al. 2010).

Investigations of the diatom flora of the Black Sea go as far back as the works of Mereschkowsky (1902), whose research resulted in the description of some globally distributed diatom genera and species (e.g, *Catenula* Mereschkowsky, *Licmosphenia* and *Stauronella*). Research on the Black Sea diatom assemblages was continued by Proshkina-Lavrenko (1955, 1963) with several new species and varieties described (e.g., *Amphora inconspicua* and *Nitzschia rupestris*). Later on, Guslyakov et al. (1992) produced an atlas of benthic diatoms for the Northwestern Black Sea extensively illustrated with electron microscope images. More recently, Witkowski et al. (2010) revised *Navicula pontica* (Mereschkowsky) A.Witkowski, M.Kulikovskiy, E.Nevrova and Lange-Bertalot 2010 and *Navicula parapontica*, A.Witkowski, M.Kulikovskiy, E.Nevrova and Lange-Bertalot 2010, whereas Witkowski et al. (2014) described *Navicula petrovii* Nevrova, Witkowski, Kociolek and Lange-Bertalot. Nevrova et al. (2013) studied *Lyrella* and described five novel species including *Lyrella abruptapontica*, *L. karayevae* and *L. pontieuxinii*. The Black Sea is inhabited by what seems to be an endemic taxon of the blue-pigment producing diatom, *Haslea karadagensis* Davidovich, Gastineau and Mouget (Davidovich et al. 2012a; Gastineau et al. 2012a, 2012b). An increasing

number of studies on the biodiversity and species richness of the Black Sea diatoms have been published in recent years (Nevrova 2022, 2023; Nevrova and Petrov 2019a, 2019b; Zidarova et al. 2022b). Strains of diatoms from the Black Sea have also been used to investigate either their patterns of auxosporulating (Podunay et al. 2021; Davidovich et al. 2012b, 2017a, 2017b, 2019; Kaczmarska et al. 2018), physiology (Bedoshvili et al. 2021; Davidovich et al. 2016, 2018; Podunay et al. 2016) or genomic peculiarities (Gastineau et al. 2021).

From the list above, it is obvious that it is mostly the northern part of the Black Sea whose diatom communities have been investigated and in contrast, the Southern Turkish Coasts of the Black Sea only received attention very recently (Baytut 2013). The latter authors investigated the discharge zone of the Kizilirmak River into the Black Sea and among the diatom species list many new records for Turkey were published. Similarly, Kaleli et al. (2017) studied Akliman city in the Sinop area and provided a species list also with new records for Turkish waters.

In this article, we contribute to the expanding list of novel taxa by describing *Craspedostauros nazmii* sp. nov., a new epilithic species from the Turkish Coasts of the Black Sea. The results are based on light and Scanning Electron Microscopy. This is the first and, for now, only species of *Craspedostauros* observed along the Turkish Black Sea coast.

Material and methods

The sample was collected in July 2017 from epilithic substrata in Kastamonu Doganyurt, Southern Black Sea (42°0'29.24"N, 33°27'34.19"E) (Fig. 1). A sin-

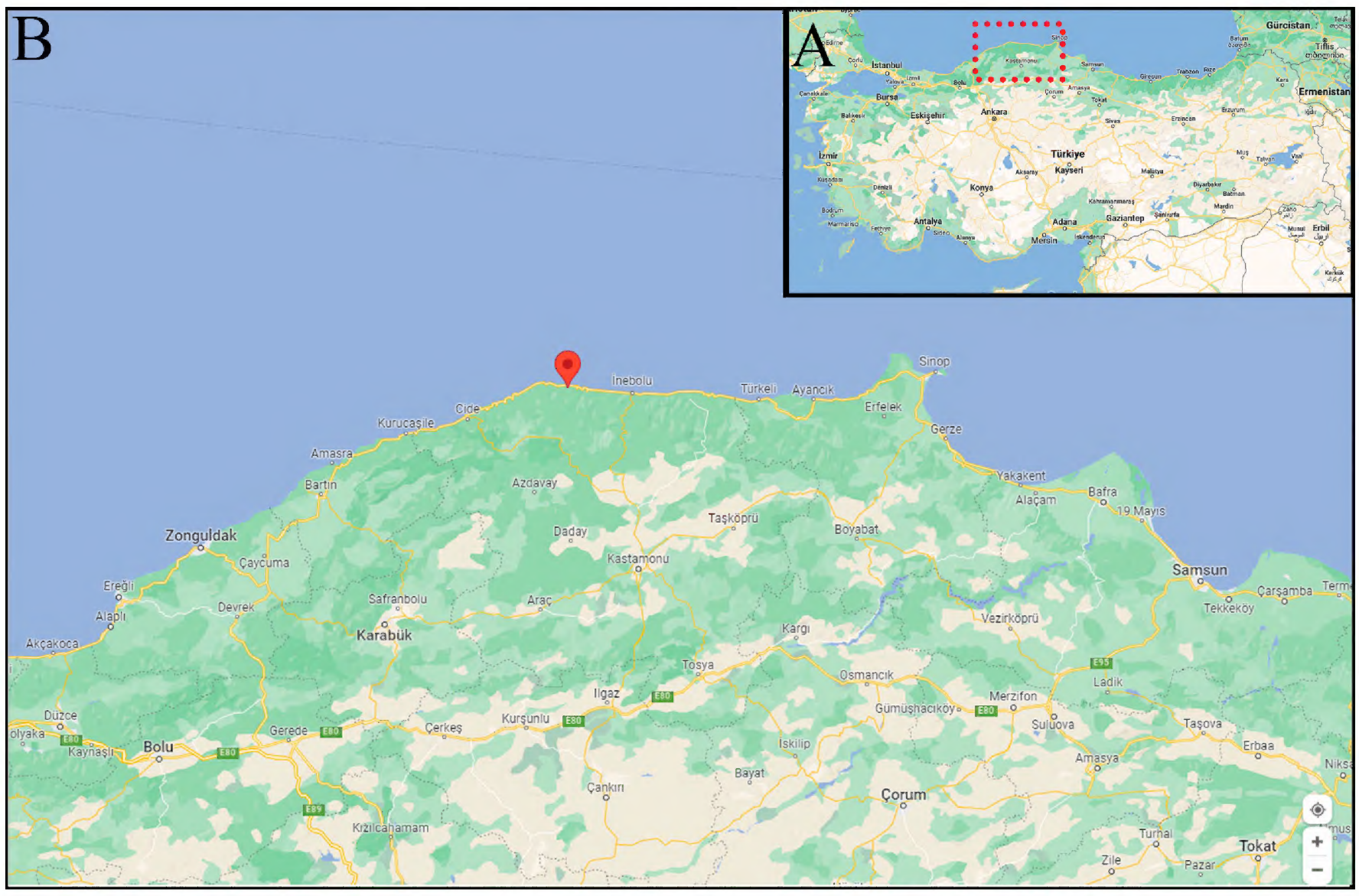

Figure 1. Map of the sampling location **A** shows the Kastamonu Province (red rectangle) on the shores of the Black Sea. The red dot on **B** indicates the exact place where the sampling was conducted in Doğanyurt, north of Kastamonu. Figures obtained from Google Maps, Creative Commons CCO Licence, GNU Free Document Licence.

gle epilithic sample was collected using a toothbrush from the surfaces of submerged stones of this sampling station. Environmental parameters were measured using a Lange Hach HQ40d. No live observations of the samples were conducted as the sample was processed directly and boiled with H_2O_2 and 10% HCl to remove organic matter and calcium carbonate respectively. After washing the diatoms with distilled water several times, permanent slides were mounted with Naphrax synthetic resin. Light Microscope (LM) observations were conducted on an OLYMPUS BX51 Light Microscope with OLYMPUS EP50 camera at Kütahya Dumlupınar University. Scanning Electron Microscope (SEM) observations were made using a FEI Versa 3D at İstanbul University with secondary electron and backscatter excitation, 10 kV and a working distance 10 mm. For this purpose, samples were placed on polycarbonate membrane filters with a 5 µm mesh. The membranes were left to dry and then attached to aluminum stubs with double-sided carbon tape, and sputter coated with ca. 20 nm gold using a Turbo–Pumped Quorum Q 150OT ES coater.

Results

Craspedostauros nazmii **E.Yılmaz, Witkowski, Solak, sp. nov.**
Figs 2, 3

Type material. ***Holotype*****:** Slide Number SZCZ 28843, collection of Andrzej Witkowski at the University of Szczecin. Valves representing the holotype population illustrated in Fig. 2F.

Isotype**:** Slide number TR_Kastamonu_Doganyurt_EPL_Tem2017 deposited in Kütahya Dumlupınar University (Turkey).

Registration. http://phycobank.org/103900.

Type locality. Turkey, Kastamonu Province, seashore in Doğanyurt District, (42°0'29.24"N, 33°27'34.19"E), collected by: Cüneyt Nadir Solak, July 18, 2017.

Description. LM (Fig. 2A–M) valves lanceolate to narrow lanceolate, slightly constricted in the middle and with rostrate to subcapitate apices, 29–42 µm in length, 4.5–5.5 µm in width (n = 50). Valves with a slight constriction in the middle, tapering towards narrowly rostrate to subcapitate apices. Axial area very narrow, but distinct, in the valve middle expanding into a central area in a form of stauros encompassing the whole valve width. Raphe branches in LM resolvable, slightly undulate, external proximal raphe endings distinct, tear-like shaped, external distal raphe endings strongly bent in same direction. Transapical striae well resolvable in LM, parallel in the middle, becoming slightly radiate and finally divergent close to apices, 20–21 in 10 µm (Figs 2A–M, 3A–D).

SEM (Fig. 3A–H). Valve external view (Fig. 3A–D), valve face flat composed of one to two rows of areolae. The valve face margin marked by a distinct, continuous apically oriented siliceous rib (transformed vimineae). The transition from the valve face to valve mantle gradual in the valve middle, becoming abrupt at the apices. Hyaline area becoming larger towards to the margins in the centre. Transapical striae uniseriate, composed of 1–3 areolae on the valve face and 4–6 on the mantle in central area, and decreasing to 4 towards the apical mantle (Fig. 3B–D). The striae of the valve face in the apical part composed of a solitary areola, and increasing towards the valve middle to 2 and finally 3 near the stauros. Areolae variable in size, larger near the raphe with more pores

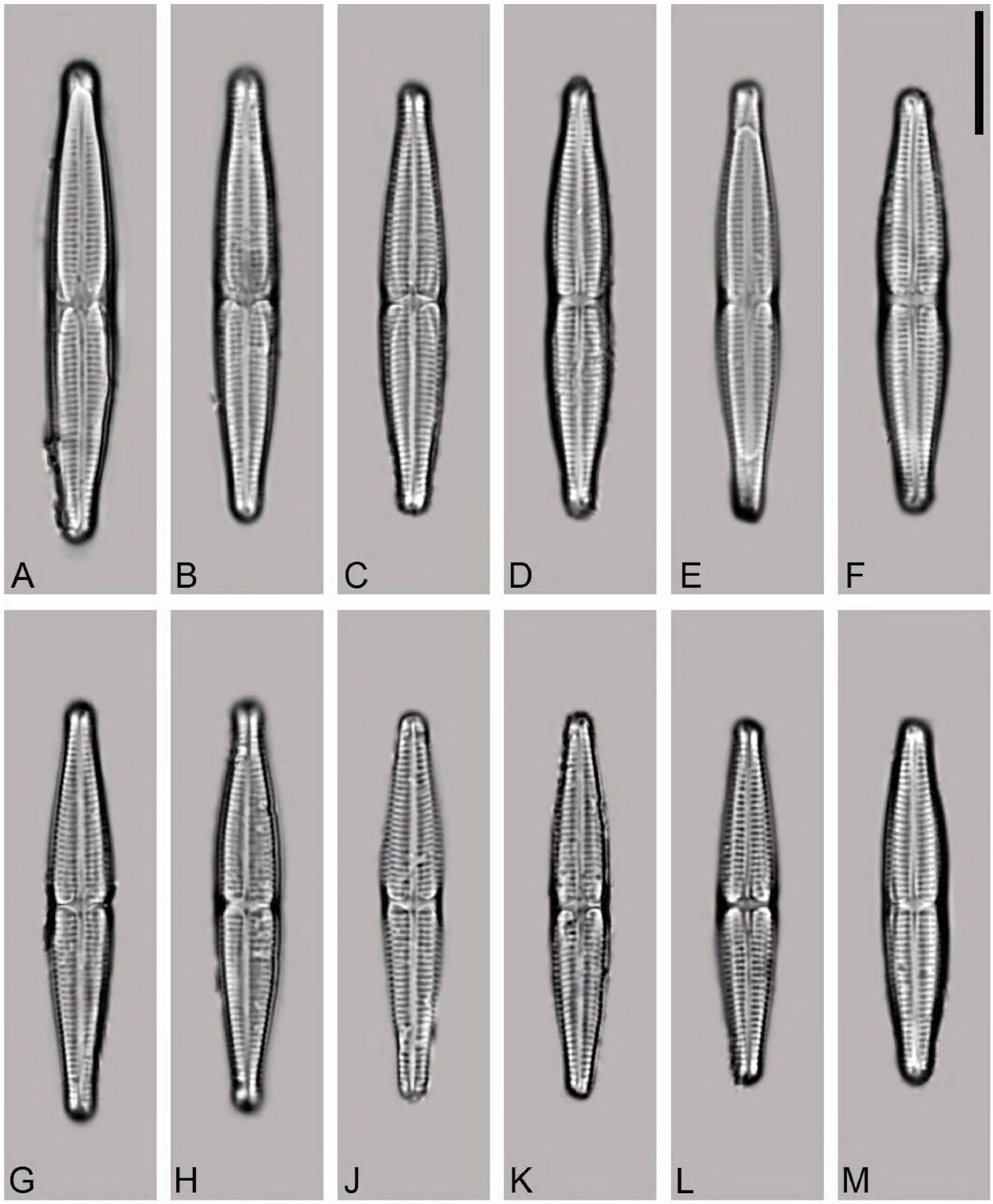

Figure 2. A–M *Craspedostauros nazmii* sp. nov., LM micrographs. Scale bar: 10 µm.

(up to 17) in the cribrate occlusions (Fig. 3B). Raphe branches slightly undulate with external proximal ends expanded, distant from each other. External apical raphe endings strongly hook-shaped. Prominent wing-like silica flaps partially covering the first row of areolae bordering the raphe sternum present near the apices at valve secondary side (Fig. 3C–D). Valve centre with hyaline area of

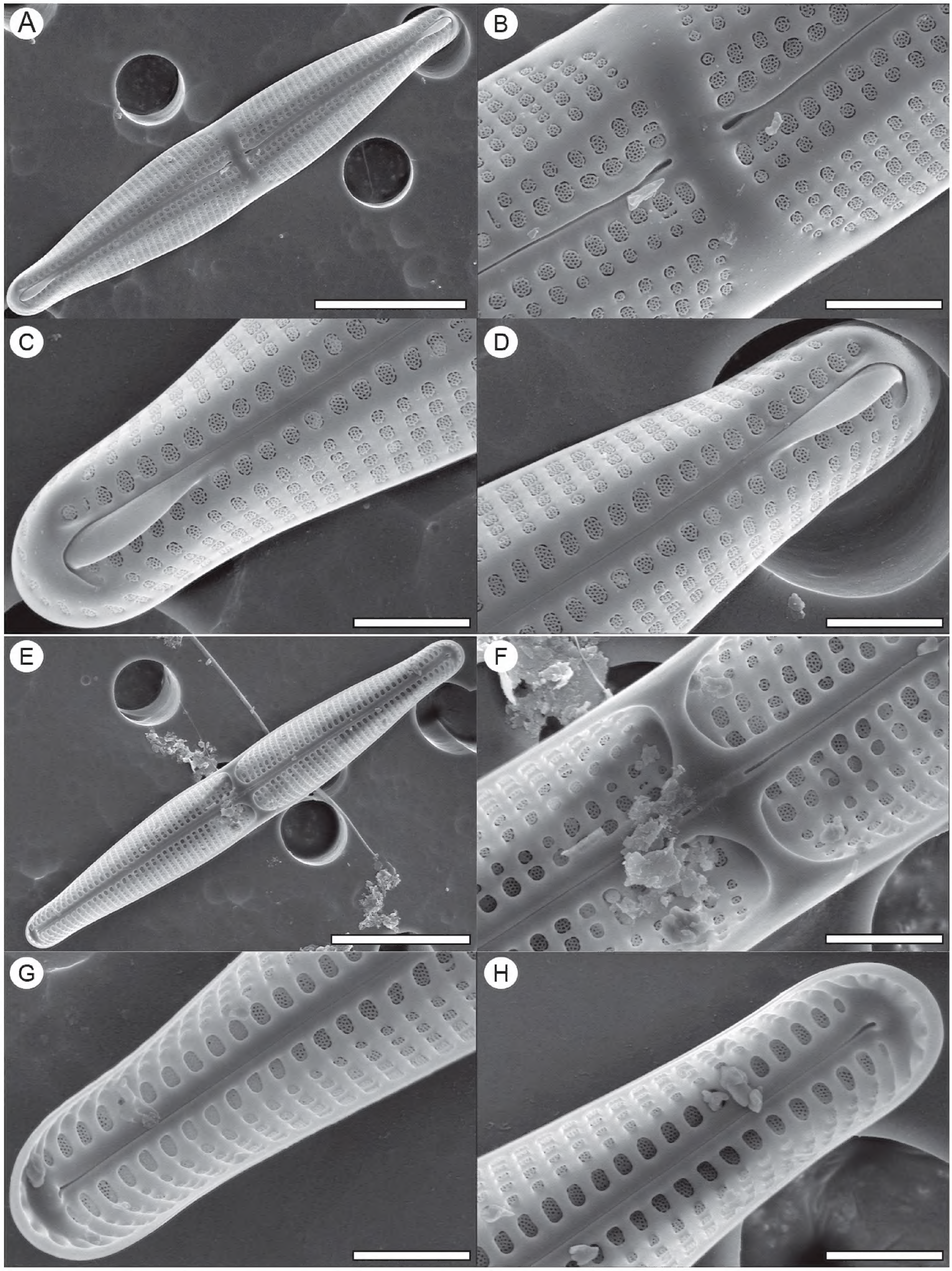

Figure 3. SEM micrographs of *Craspedostauros nazmii* sp. nov. **A** external view of entire valve **B** external view of central area **C, D** external view of valve apex showing wing-like silica flap **E** internal view of entire valve **F** internal view of central area showing raphe terminate **G–H** internal view of valve apex. Scale bars: 10 µm (**A, E**); 2 µm (**B–D, F–H**).

the stauros and symmetric with regular areolae. On one side three and on the other one to two rows of areolae at the beginning. Then, two rows of areolae on both sides and finally one row of areola towards the ends (Fig. 3A–D).

SEM (Fig. 3E–H). Valve surface internally flat, narrow pore-free longitudinal lines running from apex to apex abruptly marking the face-mantle junction (Fig. 3E). Raised stauros distinctly narrower than the fascia (Fig. 3F), broadening and decreasing in thickness close to the valve margins (Fig. 3E–F). Central internal raphe fissures terminate at slight knob of silica onto rectelevatum (Fig. 3F). A flatly ended cylindrical knob present at the central nodule. Apical raphe endings terminating within prominent helictoglossae within a relatively expanded pore-free area (Fig. 3G–H). Areolae externally occluded by cribra, appearing sunken, especially close to the raphe-sternum (Fig. 3F–H).

Etymology. This species is dedicated to Nazmi Yilmaz, father of the first author Elif Yilmaz in appreciation for his dedication to support and encourage her.

Distribution and ecology. The species was observed in Doğanyurt District, Kastamonu Province, Black Sea. The conductivity values at the sampling station were 18.69 mS cm^{-1}, DO values were 8.86 mg L^{-1}, TEMP values were 15.4 °C.

Table 1. Comparison of the main morphological and morphometric characters of *Craspedostauros nazmii* sp. nov. (n = 50) with morphologically similar taxa from the literature.

	Craspedostauros nazmii	***C. macewanii***	***C. capensis***	***C. britannicus***	***C. indubitabilis***	***C. alatus***
Valve outline	linear to narrow lanceolate, slightly constricted	linear to linear-lanceolate, slightly constricted	lanceolate, constricted	linear to narrow lanceolate	linear to linear-elliptic	linear to linear-lanceolate, slightly constricted
Valve length (µm)	29.6–41.8	26.0–51.0	25.0–35.0	14.0–60.0	25.0–60.0	20.0–37.0 (16.0–38.0)
Valve width (µm)	4.5–5.4	4.5–5.5	4.5–5.5	5.0–6.0	6.0–7.0	3.0–5.0 (5.0–7.0)
Stria density (in 10 µm)	20–21	28–31	19	~24	25–27	26–28(22–25)
Areolae size	variable	similar	variable	similar	similar	variable
Areolae larger along raphe side	yes	—	Yes	No	Yes	Yes
Average number of cribrum pores	6–17	highly variable	5–13	5(+)	—	3–11
Cribrum shape	rounded	rectangular-rounded	rectangular-rounded	rounded	rounded	rounded
Internal central raphe endings	slightly knob	rectevelatum + knob	knob	double helictoglossae	Knob	rectevelatum
Valve face: mantle junction	abrupt (distinct)	strong (distinct)	gradual	none	strong (distinct)	Strong (distinct)
Valve margin at centre	straight	straight	straight	slightly expanded	straight	very slightly expanded
Apical wing-like silica flaps	present	rudimentary	absent	absent	absent	present
References	this study	Majewska et al. 2021	Cox 1999	Cox 1999	Rivera et al. 2011	Majewska et al. 2018

Discussion

The taxa belonging in *Craspedostauros* originate from various geographic regions of the world with *Craspedostauros britannicus* E.J.Cox 1999 known

from the East and West coast of Great Britain, *C. neoconstrictus* E.J.Cox 1999 from the English Channel coasts, *C. australis* E.J.Cox 1999 from the south coast of Australia, *C. indubitabilis* (Lange-Bertalot and S.I.Genkal) E.J.Cox 1999 from Europe, North America and the Subantarctic Islands, *C. alyoubii* J.Sabir and Ashworth 2016 and *C. paradoxus* Ashworth and Lobban 2016 in the Red Sea and the West coast of Guam respectively, *C. amphoroides* (Grunow ex A.W.F.Schmidt) E.J.Cox 1999 in the Philippines, *C. decipiens* (Hustedt) E.J.Cox 1999 in the English Channel and North Sea coasts, *C. capensis* E.J.Cox 1999 along the West coast of South Africa and *C. laevissimus* (West and G.S.West) Sabbe 2003 in Maritime Antarctic saline lakes (Cox 1999; Sabbe et al. 2003; Rivera et al. 2011; Ashworth et al. 2017). Recently, *C. alatus* Majewska & Ashworth, 2018, *C. danayanus* Majewska & Ashworth, 2021, *C. legouvelloanus* Majewska & Bosak, 2021, and *C. macewanii* Majewska & Ashworth, 2021 were described as epibionts on sea turtles by Majewska et al. (2018, 2021). It is important to note that most of the recent discoveries originated from the Southern Hemisphere (e.g. Majewska et al. 2021; Zidarova et al. 2022a; Trentin et al. 2022).

Based on comparative morphology (Table 1), *C. alatus* in Majewska et al. (2018), *C. britannicus* E.J. Cox (1999), *C. capensis* E.J. Cox (1999), *C. indubitabilis* (Lange-Bertalot and S.I.Genkal) E.J.Cox in Rivera et al. (2011) and *C. macewanii* Majewska and Ashworth in Majewska et al. (2021) are similar taxa. Among them, *C. capensis* is the most similar taxon to *C. nazmii* sp. nov., with similar stria density and valve width. The valve outline and cribrate areolae are also similar (linear to linear-lanceolate), however the apices are not as strongly constricted as in *C. capensis*. When compared with other taxa, the stria density is higher in *C. britannicus* (~24 in 10 µm), *C. indubitabilis* (25–27 in 10 µm) and *C. alatus* (26–28 in 10 µm) than in *C. nazmii* (20–21 in 10 µm). Regarding valve outline, *C. nazmii* sp. nov. resembles the other listed taxa except *C. indubitabilis*. *Craspedostauros indubitabilis* has a markedly elliptic outline with wider apices (Lange-Bertalot and Genkal 1999; Rivera et al. 2011: fig. 1B, C), and a larger valve width (6–7 µm). Moreover, there is no apical wing-like silica flaps (Rivera et al. 2011: fig. 1E, F). *Craspedostauros britannicus* and *C. alatus* also have shorter valves than *C. nazmii* (14.0–60.0, 20.0–37.0 and 29.6–41.8 µm respectively), have no apical wing-like silica flaps (Cox 1999: fig. 26) and the shape of the internal raphe endings are helictoglossae in *C. britannicus* but rectevelatum in *C. alatus*. The valve margin is straight in *C. nazmii* compared to *C. alatus* and *C. britannicus*. The average number of cribrum pores is higher in *C. nazmii* (6–17 in 10 µm) than in the other taxa (5–13 in *C. capensis*, 5(+) in *C. britannicus* and 3–11 in *C. alatus*). Unfortunately, despite numerous attempts, it was impossible to find in our samples any girdle bands that could be used for taxonomy in a similar way that was introduced by Cox (1999).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: EY. Data curation: EY, AW, CNS. Funding acquisition: NÖ. Investigation: EY. Methodology: AW. Project administration: CNS, NÖ. Supervision: CNS. Visualization: EY. Writing - original draft: EY. Writing - review and editing: TD, CNS, RG, NÖ, AW.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Ashworth MP, Lobban CS, Witkowski A, Theriot EC, Sabir MJ, Baeshen MN, Hajarah NH, Baeshen NA, Sabir JS, Jansen RK (2017) Molecular and Morphological Investigations of the Stauros-bearing, Raphid Pennate Diatoms (Bacillariophyceae): *Craspedostauros* E.J. Cox, and *Staurotropis* T.B.B. Paddock, and their Relationship to the Rest of the Mastogloiales. Protist 168(1): 48–70. https://doi.org/10.1016/j.protis.2016.11.001

Baytut Ö (2013) A study on the phylogeny and phylogeography of a marine cosmopolite diatom from the southern Black Sea. Oceanological and Hydrobiological Studies 42(4): 406–411. https://doi.org/10.2478/s13545-013-0096-5

Bedoshvili Y, Podunay Y, Nikonova A, Marchenkov A, Bairamova E, Davidovich N, Likhoshway Y (2021) Lipid and fatty acids accumulation features of *Entomoneis* cf. *paludosa* during exponential and stationary growth phases in laboratory culture. Diversity (Basel) 13(10): 459. https://doi.org/10.3390/d13100459

Cox E (1999) *Craspedostauros* gen. nov., a new diatom genus for some unusual marine raphid species previously placed in *Stauroneis* Ehrenberg and *Stauronella* Meresc-hkowsky. European Journal of Phycology 34(2): 131–147. https://doi.org/10.1080/09670269910001736192

Cox EJ, Williams DM (2006) Systematics of naviculoid diatoms (Bacillariophyta): A preliminary analysis of protoplast and frustule characters for family and order level

classification. Systematics and Biodiversity 4(4): 385–399. https://doi.org/10.1017/S1477200006001940

Davidovich N, Gastineau R, Gaudin P, Davidovich OI (2012a) Sexual reproduction in the newly-described blue diatom, *Haslea karadagensis*. Fottea 12(2): 219–229. https://doi.org/10.5507/fot.2012.016

Davidovich NA, Kaczmarska I, Karpov SA, Davidovich OI, MacGillivary ML, Mather L (2012b) Mechanism of male gamete motility in araphid pennate diatoms from the genus *Tabularia* (Bacillariophyta). Protist 163(3): 480–494. https://doi.org/10.1016/j.protis.2011.09.002

Davidovich OI, Davidovich NA, Podunay YA, Shorenko KI, Witkowski A (2016) Effect of salinity on vegetative growth and sexual reproduction of algae from the genus *Ardissonea* de Notaris (Bacillariophyta). Russian Journal of Plant Physiology: a Comprehensive Russian Journal on Modern Phytophysiology 63(6): 776–782. https://doi.org/10.1134/S1021443716060030

Davidovich NA, Davidovich OI, Podunay YA, Gastineau R, Kaczmarska I, Poulíčková A, Witkowski A (2017a) *Ardissonea crystallina* has a type of sexual reproduction that is unusual for centric diatoms. Scientific Reports 7(1): 14670. https://doi.org/10.1038/s41598-017-15301-z

Davidovich NA, Davidovic OI, Podunay YA (2017b) Diatom culture collection of the Karadag scientific station (Crimea). Morskoj Biologicheskij Zhurnal 2: 18–28. https://doi.org/10.21072/mbj.2017.02.1.03

Davidovich OI, Davidovich NA, Mouget JL (2018) The effect of temperature on vegetative growth and sexual reproduction of two diatoms from the genus *Haslea* Simonsen. Russian Journal of Marine Biology 44(1): 8–13. https://doi.org/10.1134/S1063074018010030

Davidovich OI, Davidovich NA, Gastineau R, Witkowski A (2019) Sexual reproduction of the black sea diatom *Climaconeis scalaris* (Brébisson) EJ Cox. Moscow University Biological Sciences Bulletin 74(4): 200–206. https://doi.org/10.3103/S0096392519040035

Gastineau R, Davidovich NA, Bardeau JF, Caruso A, Leignel V, Hardivillier Y, Jacquette B, Davidovich OI, Rincé Y, Gaudin P, Cox EJ, Mouget J-L (2012a) *Haslea karadagensis* (Bacillariophyta): A second blue diatom, recorded from the Black Sea and producing a novel blue pigment. European Journal of Phycology 47(4): 469–479. https://doi.org/10.1080/09670262.2012.741713

Gastineau R, Hardivillier Y, Leignel V, Tekaya N, Morançais M, Fleurence J, Davidovich N, Jacquette B, Gaudin P, Hellio C, Bourgougnon N, Mouget J (2012b) Greening effect on oysters and biological activities of the blue pigments produced by the diatom *Haslea karadagensis* (Naviculaceae). Aquaculture (Amsterdam, Netherlands) 368: 61–67. https://doi.org/10.1016/j.aquaculture.2012.09.016

Gastineau R, Davidovich NA, Davidovich OI, Lemieux C, Turmel M, Wróbel RJ, Witkowski A (2021) Extreme enlargement of the inverted repeat region in the plastid genomes of diatoms from the genus *Climaconeis*. International Journal of Molecular Sciences 22(13): 7155. https://doi.org/10.3390/ijms22137155

Guslyakov N, Zakordonez O, Gerasimuk V (1992) Atlas diatomovyh vodoroslei bentosa severo-zapadnoi chasti Chernogo morya i prilegayushih vodoemov (Atlas of diatom algae of benthos of the north-western part of Black Sea and adjacent waters). Naukova Dumka, Kiev, 115 pp.

Kaczmarska I, Ehrman JM, Davidovich NA, Davidovich OI, Podunay YA (2018) Structure and development of the auxospore in *Ardissonea crystallina* (C. Agardh) Grunow

demonstrates another way for a centric to look like a pennate. Protist 169(4): 466–483. https://doi.org/10.1016/j.protis.2018.05.001

Kaleli A, Akçaalan R (2021) Checklist of marine diatoms from Turkish coastal waters with updated nomenclature. Aquatic Research 4(1): 88–115. https://doi.org/10.3153/AR21008

Kaleli MA, Kulikovskiy MS, Solak CN (2017) Some new records for marine diatom flora of Turkey from Akliman, Sinop (Black Sea). Turkish Journal of Fisheries and Aquatic Sciences 17(6): 1387–1395. https://doi.org/10.4194/1303-2712-v17_6_32

Krammer K, Lange-Bertalot H (1986) Bacillariophyceae. Süsswasserflora von Mitteleuropa. G. Fischer, Jena.

Lange-Bertalot H, Genkal SI (1999) Diatoms from Siberia I. Islands in the Arcic Ocean (Yugorsky Shar Strait). Iconographia Diatomologica 6: 273.

Majewska R, Ashworth M, Lazo-Wasem E, Ronbinson NT, Ŕojas L, van de Vijver B, Pinou T (2018) *Craspedostauros alatus* sp. nov., a new diatom (Bacillariophyta) species found on museum sea turtle specimens. Diatom Research 33(2): 229–240. https://doi.org/10.1080/0269249X.2018.1491426

Majewska R, Ashworth MP, Bosak S, Goosen WE, Nolte C, Filek K, Van de Vijver B, Taylor JC, Manning SR, Nel R (2021) On sea turtle-associated *Craspedostauros* (Bacillariophyta), with description of three novel species. Journal of Phycology 57(1): 199–218. https://doi.org/10.1111/jpy.13086

Mann DG, Trobajo R, Sato S, Li C-L, Witkowski A, Rimet F, Ashworth MP, Hollands RM, Theriot EC (2021) Ripe for reassessment: A synthesis of available molecular data for the speciose diatom family Bacillariaceae. Molecular Phylogenetics and Evolution 158: 106985. https://doi.org/10.1016/j.ympev.2020.106985

Mereschkowsky C (1902) Note sur quelques Diatomées de la Mer Noire. Le Journal de Botanique 16: 319–324.

Nevrova E (2022) Benthic diatoms of the Black Sea: rare, invasive, extinct species and assessment of taxonomic exclusivity. Voprosy sovremennoi algologii (Issues of modern algology) 2: 46–56. https://doi.org/10.33624/2311-0147-2022-2(29)-46-56

Nevrova E (2023) Taxonomic structure and diversity of benthic diatoms (Bacillariophyta) in the Northern shelf of the Black sea. Phycology 3(3): 337–355. https://doi.org/10.3390/phycology3030022

Nevrova E, Petrov A (2019a) Benthic diatoms species richness at Dvuyakornaya Bay and other coastal sites of Crimea (the Black Sea) under various environments. Mediterranean Marine Science 20(3): 506–520. https://doi.org/10.12681/mms.20319

Nevrova E, Petrov A (2019b) Assessment of benthic diatoms taxonomic diversity at coastal biotopes with different anthropogenic impact (Crimea, the Black Sea). Turkish Journal of Botany 43(5): 608–618. https://doi.org/10.3906/bot-1903-43

Nevrova E, Witkowski A, Kulikovskiy M, Lange-Bertalot H, Kociolek JP (2013) A revision of the diatom genus *Lyrella* Karayeva (Bacillariophyta: Lyrellaceae) from the Black Sea, with descriptions of five new species. Phytotaxa 83(1): 1–38. https://doi.org/10.11646/phytotaxa.83.1.1

Podunay YA, Davidovich OI, Davidovich NA (2016) Effect of culture density on sexual reproduction of *Ardissonea crystallina* (Bacillariophyta) inhabiting the Black Sea. Moscow University Biological Sciences Bulletin 71(2): 82–86. https://doi.org/10.3103/S0096392516020085

Podunay YA, Davidovich NA, Davidovich OI, Witkowski A, Gastineau R, Solak CN (2021) The sexual reproduction and life cycle of the pennate diatom *Entomoneis* cf. *paludosa* (W. Smith) Reimer (Bacillariophyta). Russian Journal of Marine Biology 47(1): 19–28. https://doi.org/10.1134/S1063074021010089

Proshkina-Lavrenko AI (1963) Diatoms algae of Black Sea benthos, AN SSSR Press, Moscow, Leningrad. [In Russian]

Proshkina-Lavrenko AI (1955) Diatoms plankton of the Black Sea, AN SSSR Press, Moscow, Leningrad. [In Russian]

Risjani Y, Witkowski A, Kryk A, Yunianta, Górecka E, Krzywda M, Safitri I, Sapar A, Dąbek P, Arsad S, Gusev E, Rudiyansyah, Peszek Ł, Wróbel RJ (2021) Indonesian coral reef habitats reveal exceptionally high species richness and biodiversity of diatom assemblages. Estuarine, Coastal and Shelf Science 261: 107551. https://doi.org/10.1016/j.ecss.2021.107551

Rivera P, Cruces F, Ector L (2011) Comentarios y observaciones acerca de la diatomea *Craspedostauros indubitabilis* (Lange-Bertalot and Genkal) EJ Cox encontrada por primera vez en aguas marinas costeras de Chile. Gayana. Botánica 68(2): 123–128. https://doi.org/10.4067/S0717-66432011000200001

Round FE, Crawford RM, Mann DG (1990) Diatoms: biology and morphology of the genera. Cambridge university press, 747 pp.

Sabbe K, Verleyen E, Hodgson DA, Vanhoutte K, Vyverman W (2003) Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. Antarctic Science 15(2): 227–248. https://doi.org/10.1017/S095410200300124X

Trentin R, Moschin E, Duarte Lopes A, Schiaparelli S, Custódio L, Moro I (2022) Molecular, morphological and chemical diversity of two new species of antarctic diatoms, *Craspedostauros ineffabilis* sp. nov. and *Craspedostauros zucchellii* sp. nov. Journal of Marine Science and Engineering 10(11): 1656. https://doi.org/10.3390/jmse10111656

Witkowski A, Lange-Bertalot H, Metzeltin D (2000) Diatom Flora of Marine Coasts I. In: Lange-Bertalot H (Ed.) Icon Diatoml 7. Koeltz Scientific Books, Konigstein, 925 pp.

Witkowski A, Kulikovskiy M, Nevrova E, Lange-Bertalot H, Gogorev R (2010) The genus *Navicula* in ancient basins. I. Two novelties from the Black Sea. Plant Ecology and Evolution 143(3): 307–317. https://doi.org/10.5091/plecevo.2010.421

Witkowski A, Nevrova E, Lange-Bertalot H, Kociolek JP (2014) *Navicula petrovii* sp. nov. (Bacillariophyceae), a naviculoid diatom with amphoroid symmetry and its relationship to *Navicula* sensu stricto and other naviculoid genera. Beihefte zur Nova Hedwigia 143: 469–484.

Zidarova R, De Haan M, Ivanov P, Hineva E, Van De Vijver B (2022a) The genus *Craspedostauros* E. J. Cox (Bacillariophyta) on the coasts of Livingston Island, Maritime Antarctica. Phytotaxa 572(1): 1–24. https://doi.org/10.11646/phytotaxa.572.1.1

Zidarova R, Ivanov P, Hristova O, Dzhurova B, Hineva E (2022b) The unexpected diversity in *Amphora sensu lato* (Bacillariophyta) at Sozopol Bay, the western Black Sea. Phytotaxa 544(2): 103–127. https://doi.org/10.11646/phytotaxa.544.2.1